

RESEARCH ARTICLE

# Combining Ability of Different Agronomic Traits and Yield Components in Hybrid Barley

Xinzhong Zhang<sup>1,2,3,4</sup>✉, Liangjie Lv<sup>1,2,3,4</sup>✉, Chao Lv<sup>1,2,3,4</sup>, Baojian Guo<sup>1,2,3,4</sup>, Rugen Xu<sup>1,2,3,4</sup>\*

**1** Jiangsu Key Laboratory of Crop Genetics and Physiology, Yangzhou University, Yangzhou, China, **2** Co-Innovation Center for Modern Production Technology of Grain Crops, Yangzhou University, Yangzhou, China, **3** Key Laboratory of Plant Functional Genomics of the Ministry of Education, Yangzhou University, Yangzhou, China, **4** Institute of Barley Research, Yangzhou University, Yangzhou, China

✉ These authors contributed equally to this work.

\* [rgxu@yzu.edu.cn](mailto:rgxu@yzu.edu.cn)



**OPEN ACCESS**

**Citation:** Zhang X, Lv L, Lv C, Guo B, Xu R (2015) Combining Ability of Different Agronomic Traits and Yield Components in Hybrid Barley. PLoS ONE 10(6): e0126828. doi:10.1371/journal.pone.0126828

**Academic Editor:** Meixue Zhou, University of Tasmania, AUSTRALIA

**Received:** January 14, 2015

**Accepted:** April 8, 2015

**Published:** June 10, 2015

**Copyright:** © 2015 Zhang et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data Availability Statement:** All relevant data are within the paper and its Supporting Information files.

**Funding:** This work was funded by the National Natural Science Foundation of China (30971779, 31071407, 31128014), the National Barley and Highland Barley Industrial Technology Specially Constructive Foundation of China (CARS-05), the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD), and the Scientific Research Initial Fund for New Researchers in Yangzhou University. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

## Abstract

Selection of parents based on their combining ability is an effective approach in hybrid breeding. In this study, eight maintainer lines and nine restorer lines were used to obtain 72 crosses for analyzing the general combining ability (GCA) and special combining ability (SCA) for seven agronomic and yield characters including plant height (PH), spike length excluding awns (SL), inter-node length (IL), spikes per plant (SP), thousand kernel weight (TKW), kernel weight per plant (KWP) and dry matter weight per plant (DWP). The results showed that GCA was significantly different among parents and SCA was also significantly different among crosses. The performance of hybrid was significantly correlated with the sum of female and male GCA (TGCA), SCA and heterosis. Hu1154 A, Mian684 A, 86F098 A, 8036 R and 8041 R were excellent parents with greater general combining ability. Five crosses, Hu1154 A×8032 R, Humai10 A×8040 R, Mian684 A×8037 R, Mian684 A×8041 R and 86F098 A×8037 R, showed superior heterosis for most characters.

## Introduction

Barley (*Hordeum vulgare* L.) ranks the fourth in terms of planting area and total production among all cereal crops in the world [1]. It has been widely used as a health food, animal feed and fermentable material for the beer industry. Great progress has been made on barley heterosis studies [2] with the development of barley three-line breeding system based on cytoplasmic male sterility (CMS), maintainer and restorer lines [3]. The first commercial hybrid variety ‘Colossus’ was released in the UK in 2002 [4]. Since then, Syngenta Ltd released more than ten six-row winter hybrid barley varieties based on the CMS system. Over 200,000 ha of hybrid barley varieties were sown in Europe [4].

Heterosis exists widely in barley hybrids but varies greatly among crosses [2]. The mid-parent heterosis of barley grain yield ranged from 0.7 to 19.9% among different hybrids with an average value of 11.3%, while better-parent heterosis ranged from -1.7 to 18.3% with a slightly lower value of 9.2% [5]. Hence, selection of hybrids with superior heterosis from a large

**Competing Interests:** The authors have declared that no competing interests exist.

number of crosses is cost-effective in breeding programs. One of the key issues for the successful use of hybrid barley is to identify parents that have a high combining ability for producing hybrids with greater heterosis.

Evaluation of all possible crosses are time-consuming and laboursome in breeding programs. Certain lines have the ability to combine well with other lines, suggesting that these lines have good GCA. When an inbred combines well only in certain crosses, that means that it has good SCA [6]. Combining ability is effective for the selection of excellent parents in early generations [7]. GCA provides a simple approach to predict additive effects contributing to heterosis [8] and SCA also plays an important role on heterosis [9]. Combining ability has been successfully used to identify superior combinations in rice [10,11], maize [12,13,14] and wheat [15,16]. In barley, combining ability has been reported for various traits, including spike traits [17], flour pasting properties [18], salinity tolerance [19], and waterlogging tolerance [20]. Parents having high GCA values could be used to produce improved lines in hybridization programs and better hybrids can be produced in combination with high SCA values [17]. A moderate and significant correlation between mid-parent and hybrid performance and slightly lower correlation between the sum of GCA effects and performance of the hybrid itself were found when using 124 six-rowed winter barley hybrids based on CMS × restorer to examine the potential in predicting the hybrid performance of grain yield based on mid-parent values or GCA effects [5].

The objectives of this study were to: 1) study combining ability of different agronomic traits and yield components; and 2) study the relationships between heterosis and combining ability thus to provide a theoretical basis for parent selection in the use of hybrid varieties.

## Materials and Methods

### Materials and field experiment

Eight CMS lines (A) and nine restorer lines (R) (Table 1) were used to make 72 hybrids. All the lines were sourced from the Barley Research Institution of Yangzhou University.

The experiment was performed at the Experimental Farm of Yangzhou University (119.4°E, 332.3°N) in the 2011 growing season. All 72 possible hybrids were produced by manual pollination. Forty seeds of each parent and hybrid were sown in a 5-row plot with a 1.2 m row-length and 20 cm between rows. The experiment was arranged in three replicates. For all trials, the fertilizer used included: 150 kg/ha before sown, 75 kg/ha at seedling stage and 75 kg/ha used at elongation stage. Aphids were sprayed at both seedling and flowering stages. Pinoxaden was applied to control weeds before winter. At maturity, eight plants were randomly taken from the middle line for the measurements of seven traits: plant height (PH), spike length

**Table 1. The hybrid barley parents and their row type in this experiment.**

No.	Male sterile line	Row type	No.	Restoration line	Row type
A <sub>1</sub>	Sunong5078A	Two row	R <sub>1</sub>	8032R	Six row
A <sub>2</sub>	Hu1154A	Two row	R <sub>2</sub>	8033R	Six row
A <sub>3</sub>	Humai10A	Two row	R <sub>3</sub>	8034R	Two row
A <sub>4</sub>	89-0915A	Two row	R <sub>4</sub>	8035R	Two row
A <sub>5</sub>	Sunong5266A	Two row	R <sub>5</sub>	8036R	Two row
A <sub>6</sub>	Mian684A	Six row	R <sub>6</sub>	8037R	Two row
A <sub>7</sub>	84-161A	Two row	R <sub>7</sub>	8040R	Six row
A <sub>8</sub>	86F098A	Six row	R <sub>8</sub>	8041R	Six row
			R <sub>9</sub>	8042R	Two row

doi:10.1371/journal.pone.0126828.t001

excluding awns (SL), inter-node length (IL), spikes per plant (SP), thousand kernel weight (TKW), kernel weight per plant (KWP) and dry matter weight per plant (DWP).

## Statistical analysis

Based on the average value of eight plants, mid-parent (MP) and over-better-parent (OBP) heterosis for all traits were calculated by the formulae: MP heterosis =  $F_1 - [(P_1 + P_2) / 2]$  and OBP heterosis =  $F_1 - P_b$ , where  $P_b$  stands for performance of the better parent [21,22]. General combining ability and special combining ability were calculated by the formulae:

$g_i = \bar{y}_{i..} - \bar{y}$ ,  $g_j = \bar{y}_{.j} - \bar{y}$ ,  $s_{ij} = \bar{y}_{ij} - \bar{y}_{i.} - \bar{y}_{.j} + \bar{y}$ , where  $g_i$  and  $g_j$  stand for GCA of parent,  $s_{ij}$  stands for SCA of cross,  $\bar{y}_{i.}$ ,  $\bar{y}_{.j}$ ,  $\bar{y}_{ij}$  and  $\bar{y}$  stand for the mean of crosses with same parent  $P_i$ , the mean of crosses with same parent  $P_j$ , the mean of crosses  $P_i/P_j$ , the mean of all crosses, respectively [23]. Descriptive statistics, ANOVA and correlation analysis were implemented using software Matlab 2010.

## Results

### Heterosis of different crosses

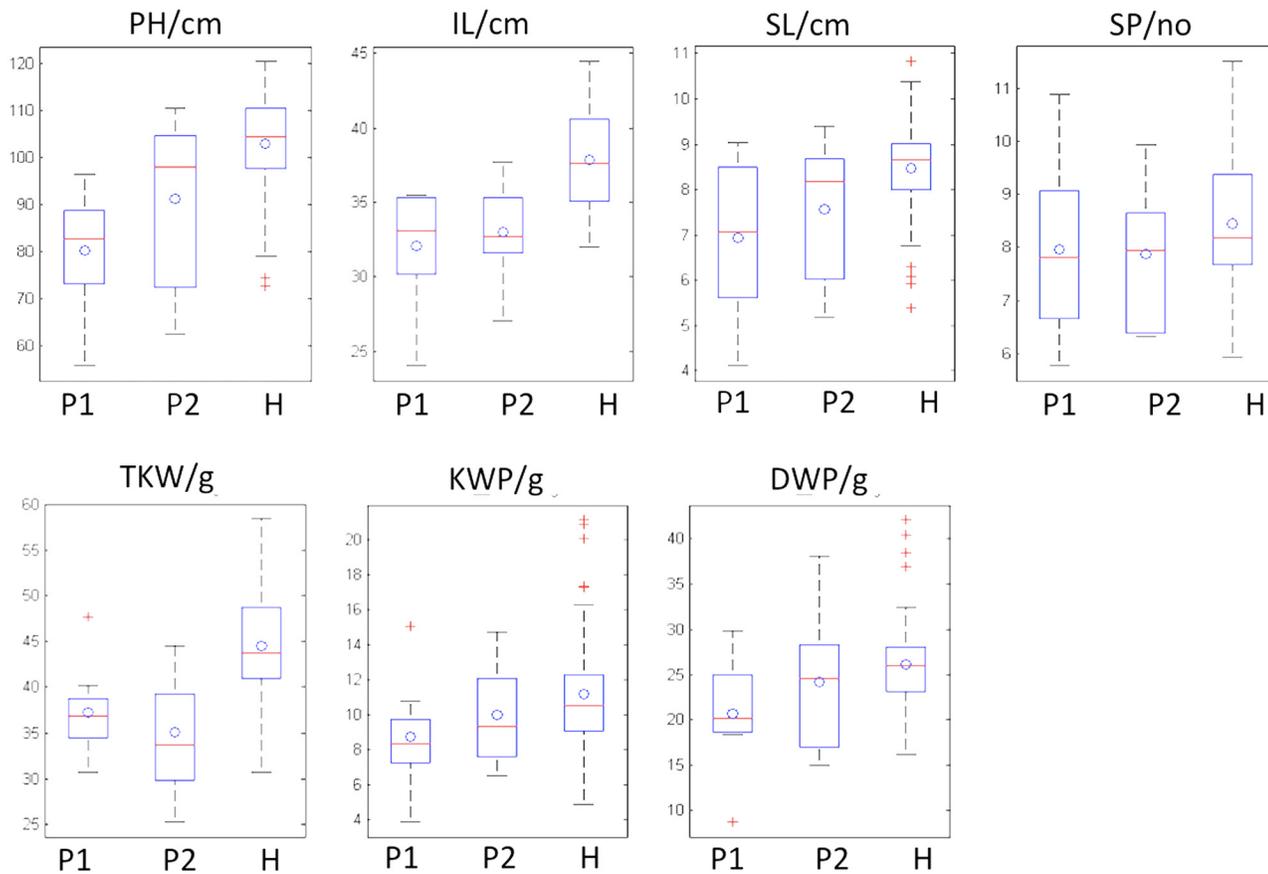
Heterosis was found in all crosses, for all measured barley traits (Fig 1). Significant differences were found among crosses for both MP and OBP heterosis. The degrees of variation for MP heterosis and OBP heterosis varied greatly among traits (Table 2) with the coefficient of variation ranging from 66.29 in SL to 223.34 in SP for MP heterosis and from 39.89 in PH to 3284.30 in KWP for OBP heterosis. The percentage of hybrids with significant heterosis ranged from 15.3% in SP to 97.2% in PH for MP heterosis and from 0% in PH to 72.2% in TKW for OBP heterosis.

### Combining ability

ANOVA of combining ability showed the variances of GCA were significant for all traits in both female and male parents (Table 3). The variances of SCA were significant only for traits PH, IL, SL and TKW. The ratio of TGCA/SCA ranged from 6.24 in IL to 18.87 in SP, indicating that additive effects played a more important role than non-additive effects for all traits.

The GCA of different varieties varied significantly among traits (Table 4). For example, the GCA of Sunong5078A was negative for IL, SL, KWP and DWP but positive for SP. Except for PH (higher PH leading to a greater chance of lodging), high positive GCAs are preferred for all the other six traits. Four parents, 89-0915A, 8032R, 8040R and 8042R, were better for PH. Seven parents, Hu1154A, Suning5266A, 86F098A, 8033R, 8035R, 8036R and 8041R, were better for IL. Eight parents, Hu1154A, Humai10A, Sunong5266A, 86F098A, 8034R, 8035R, 8037R and 8041R were better for SL. Five parents, Sunong 5078A, Hu1154A, Humai10A, 8036R and 8037R, were better for SP. Six parents, Hu1154A, 89-0915A, Sunong5266A, 8033R, 8036R and 8041R, were better for TKW. Three parent, Mian684A, 86F098A and 8041R, were better for KWP and DWP. In terms of the performance of all traits, Hu1154A, Mian684, 86F098A, 8036R and 8041R had a preferred GCA for breeding programs.

Forty eight crosses had a preferred SCA for at least one trait (S1 Table). Several crosses showed preferred SCA for PH, IL, SL, SP, TKW and DKW, respectively (Table 5). Hu1154A, Mian684A, 86F098A, 8032R, 8033R and 8040R had a preferred SCA in more crosses for different traits. Five crosses, Hu1154A×8032R, Humai10A×8040R, Mian684A×8037R, Mian684A×8041R and 86F098A×8037R, had a preferred SCA for at least three traits. The two parents of those five crosses all had different row types.



**Fig 1. Box plots for performances of parents and crosses for seven measured traits.** P1: female parents; P2: male parents; H: hybrids. The circle ‘o’ stands for mean value. The plus sign ‘+’ stands for outliers. The upper and lower lines outside the box stand for max and min adjacent value, respectively. The line inside the box stands for median value. The upper and lower hinge of the box stand for 75% and 25% percentile, respectively.

doi:10.1371/journal.pone.0126828.g001

**Table 2. Performance of different characters of hybrid barleys.**

Traits	Mid-parents heterosis				Over-better-parent heterosis			
	Mean	Range	CV	Significant percentage	Mean	Range	CV	Significant percentage
PH/cm	17.22	2.09~34.00	42.87	97.2%	27.36	8.03~57.93	39.89	0%
IL/cm	5.29	-0.20~12.64	56.43	81.9%	3.29	-2.89~9.88	92.03	68.1%
SL/cm	1.21	-0.54~2.83	66.29	76.4%	0.28	-1.54~2.46	277.56	20.8%
SP/no	0.53	-1.87~3.17	223.34	15.3%	-0.41	-2.97~2.39	324.69	5.6%
TKW/g	8.31	-1.50~20.77	69.59	73.6%	4.90	-9.04~18.16	125.95	72.2%
KWP/g	1.78	-3.08~9.75	130.96	16.7%	0.09	-7.21~7.29	3284.30	9.7%
DWP/g	3.68	-6.96~16.41	130.32	33.3%	-0.54	-15.92~9.75	1110.07	8.33%

PH: plant height; SL: spike length excluding awns; IL: inter-node length; SP: spikes per plant; TKW: thousand kernel weight; KWP: kernel weight per plant; DWP: dry matter weight per plant.

doi:10.1371/journal.pone.0126828.t002

**Table 3. ANOVA of combining ability for different traits (*F value*).**

	PH	IL	SL	SP	TKW	KWP	DWP
Female GCA	27.20**	14.69**	46.10**	9.38**	29.52**	16.17**	11.62**
Male GCA	81.72**	32.95**	47.60**	6.09**	28.41**	4.05**	6.57**
SCA	7.13**	7.64**	5.62**	0.82	5.37**	1.18	1.30
GCA/SCA	15.28	6.24	16.67	18.87	10.79	17.14	13.99

\*, \*\* significant at  $p < 0.05, 0.01$  respectively.

GCA: general combining ability; SCA: special combining ability

doi:10.1371/journal.pone.0126828.t003

### Correlation between hybrid performance, heterosis and combining ability

Significant correlation was found between combining ability and heterosis (Table 6). For all traits, both MP and OBP heterosis were significantly correlated with SCA. For the yield components SP, TKW and KWP, heterosis was also significantly correlated to total GCA (the sum of female GCA and male GCA, TGCA). The performance of hybrids had a significant correlation with heterosis and combining ability (Table 7). The correlation coefficients between hybrid performance with heterosis were slightly lower than those between hybrid performance with combining ability. The correlation coefficients between hybrid performance with TGCA were much higher than those between hybrids performance with SCA for all traits except IL.

**Table 4. General combining ability for agronomic and yield characters.**

Parents	PH	IL	SL	SP	TKW	KWP	DWP
Sunong5078A	0.47	-2.48**	-0.54**	1.13**	-0.98	-1.27*	-1.72*
Hu1154A	0.91	1.34**	0.82**	1.04**	4.64**	-0.27	-0.57
Humai10A	4.96**	-0.06	0.56**	0.88**	0.81	0.69	1.57
89-0915A	-9.07**	-0.89**	-0.69**	0.15	4.22**	-3.28**	-3.70**
Sunong5266A	1.78*	1.05**	0.40**	-0.96**	1.28*	-0.57	-0.66
Mian684A	-0.75	0.23	-0.75**	-1.06**	-2.66**	2.24**	2.02*
84-161A	-1.42	0.21	0.02	-0.48	-2.88**	-2.04**	-2.79**
86F098A	3.11**	0.61*	0.19*	-0.69*	-4.44**	4.48**	5.84**
PLSD <sub>0.05</sub>	1.50	0.59	0.16	0.56	1.14	1.14	1.68
PLSD <sub>0.01</sub>	1.99	0.78	0.22	0.74	1.52	1.52	2.23
8032R	-10.50**	-0.63*	-1.15**	-0.44	-1.91**	1.02	0.47
8033R	6.21**	2.72**	0.09	-0.31	2.34**	0.58	1.76
8034R	2.38**	-2.21**	0.97**	-0.63*	0.00	-1.81**	-3.33**
8035R	4.22**	1.44**	0.19*	0.11	-1.29*	-0.30	-2.08*
8036R	3.38**	1.15**	-0.07	1.16**	5.35**	-0.45	0.65
8037R	1.47	-2.76**	0.47**	1.24**	-2.24**	-1.37*	-1.26
8040R	-6.45**	-0.59	-0.43**	-1.02**	-1.38*	0.05	-1.01
8041R	10.78**	2.07**	0.52**	-0.43	4.54**	2.60**	5.11**
8042R	-11.50**	-1.19**	-0.60**	0.31	-5.41**	-0.32	-0.31
PLSD <sub>0.05</sub>	1.60	0.63	0.18	0.60	1.22	1.22	1.79
PLSD <sub>0.01</sub>	2.13	0.84	0.23	0.79	1.62	1.62	2.38

\*, \*\* significant at  $p < 0.05, 0.001$  respectively.

See Table 2 for trait abbreviations

doi:10.1371/journal.pone.0126828.t004

**Table 5. Crosses with beneficial special combining ability for the seven traits.**

PH	IL	SL	SP	TKW	KWP	DWP
A1×R2	A1×R1	A1×R1	A1×R4	A1×R9	A6×R7	A2×R1
A1×R5	A1×R7	A2×R1	A2×R1	A2×R1	A6×R8	A6×R8
A1×R9	A2×R1	A2×R3		A2×R2	A8×R2	A8×R9
A2×R8	A2×R2	A2×R4		A2×R7		
A3×R4	A2×R7	A3×R7		A2×R8		
A3×R6	A3×R1	A4×R2		A3×R2		
A4×R1	A3×R7	A5×R1		A3×R7		
A4×R5	A4×R2	A5×R9		A4×R9		
A4×R7	A4×R8	A6×R2		A6×R3		
A6×R1	A4×R9	A6×R6		A6×R5		
A6×R7	A5×R2	A6×R8		A6×R6		
A7×R3	A6×R4	A7×R9		A7×R7		
A7×R6	A6×R5	A8×R4		A8×R3		
A8×R1	A6×R6	A8×R5		A8×R6		
A8×R2	A7×R1	A8×R6				
A8×R8	A7×R2					
	A8×R4					
	A8×R5					
	A8×R6					
	A8×R9					

See [Table 2](#) for trait abbreviations.

doi:10.1371/journal.pone.0126828.t005

**Table 6. Correlation between heterosis and combining ability.**

Traits	Heterosis	FGCA	MGCA	TGCA	SCA
PH	MP	-0.19	-0.08	-0.17	0.78**
	OBP	-0.40**	0.11	-0.09	0.68**
IL	MP	0.06	0.18	0.18	0.78**
	OBP	0.18	0.18	0.25*	0.79**
SL	MP	-0.19	-0.04	-0.15	0.70**
	OBP	0.09	-0.08	0.00	0.36**
SP	MP	0.26*	0.35**	0.42**	0.60**
	OBP	0.10	0.34**	0.30*	0.53**
TKW	MP	0.36**	0.31**	0.47**	0.65**
	OBP	0.30*	0.29*	0.42**	0.57**
KWP	MP	0.43**	0.08	0.41**	0.76**
	OBP	0.36**	-0.11	0.27*	0.71**
DWP	MP	0.15	0.12	0.19	0.57**
	OBP	0.21	-0.08	0.11	0.49**

\*, \*\* significant at p < 0.05, 0.001 respectively.

See [Table 2](#) for trait abbreviations.

FGCA: female general combining ability; MGCA: male general combining ability; TGCA: total general combining ability, TGCA = FGCA+MGCA; SCA: special combining ability.

MP: mid-parents heterosis; OBP: over-better-parent heterosis.

doi:10.1371/journal.pone.0126828.t006

**Table 7. Correlation between the performance of hybrids and combining ability.**

	MP	OBP	FGCA	MGCA	TGCA	SCA
PH	0.30**	0.31**	0.39**	0.73**	0.82**	0.57**
IL	0.70**	0.75**	0.36**	0.58**	0.68**	0.73**
SL	0.26*	0.20	0.56**	0.61**	0.83**	0.56**
SP	0.68**	0.54**	0.64**	0.55**	0.85**	0.53**
TKW	0.78**	0.69**	0.53**	0.56**	0.77**	0.64**
KWP	0.77**	0.62**	0.73**	0.39**	0.83**	0.56**
DWP	0.49**	0.38**	0.63**	0.50**	0.81**	0.59**

\*, \*\* significant at  $p < 0.05$ ,  $0.001$  respectively.

See [Table 2](#) for trait abbreviations.

FGCA: female general combining ability; MGCA: male general combining ability; TGCA: total general combining ability, TGCA = FGCA+MGCA; SCA: special combining ability.

MP: mid-parents heterosis; OBP: over-better-parent heterosis.

doi:10.1371/journal.pone.0126828.t007

## Discussion

Barley hybrid breeding has been remarkably successful in past decades. However, due to the lack of high yielding heterotic patterns and the lower selection gain for hybrid compared to traditional breeding, only a few hybrid barley varieties have been released [4]. Selection of superior hybrids based on plant performance is more practical but more time-consuming. Combining ability is considered to be a useful indirect criterion for parent selection. However, only one study on combining ability of hybrid barley grain yield has been reported to our knowledge [5]. In fact, both agronomic and yield traits are important in hybrid barley breeding programs [2]. In this study, seven important traits PH, SL, IL, SP, TKW, KWP and DWP were investigated. GCA for all traits was significant while SCA was significant only for traits PH, IL, SL and TKW. The ratio of TGCA/SCA revealed that additive effects were the main effect on barley traits, which was the same in previous studies on barley [17] and maize [12]. Therefore, it is necessary to select parents with high general GCA, which would benefit the offspring. In this study, Hu1154A, Mian684, 86F098A, 8036R and 8041R were excellent parents with greater general combining ability.

Prediction of hybrid performance and heterosis is important in hybrid barley breeding. Heterosis and combining ability are two main indexes for hybrid performance. In this study, heterosis was significantly correlated with SCA for all agronomic and yield characters, indicating non-additive effects were the main effect for heterosis. However, mid-parent heterosis ignores non-additive effect, an important criterion in hybrid performance [24]. In contrast, the correlation coefficients between hybrids performance and TGCA were higher than those between hybrids performance and heterosis, which is different from the study by Mühleisen et al. [5]. In this study, we also found that the hybrid performance had a higher correlation with TGCA than with SCA. Hence, GCA is much more important than SCA in hybrid barley breeding. Parents with high GCAs can be crossed to select superior combinations.

## Conclusion

Using combining ability to select parents is an effective approach in hybrid breeding. The current study presented the first report on the combining ability for seven main agronomic and yield characters. GCA was significantly different among parents and SCA was also significantly different among crosses. The hybrids from two parents with high GCA always showed better

hybrid performance even though SCAs were low. Thus the selection of parents should mainly be based on their GCAs.

## Supporting Information

**S1 Table. Special combining ability for agronomic and yield characters.**  
(DOCX)

## Author Contributions

Conceived and designed the experiments: XZ CL RX. Performed the experiments: XZ LL CL BG. Analyzed the data: XZ LL. Contributed reagents/materials/analysis tools: XZ LL RX. Wrote the paper: XZ LL.

## References

1. FAOSTAT (2009) Food and Agriculture Organization of the United Nations.
2. Zhang XZ, Lv LJ, LV C, Xu RG (2013) Analysis on heterosis in agronomic and yield traits of hybrid barley. *Journal of Triticeae Crops* 33(1): 39–43.
3. Ahokas H (1979) Cytoplasmic male sterility in barley. *Acta Agriculturae Scandinavica* 29(3): 219–224.
4. Longin CFH, Mühleisen J, Maurer HP, Zhang H, Cowda M, Reif JC (2002) Hybrid breeding in autogamous cereals. *Theor. Appl. Genet.* 125(6): 1087–1096.
5. Mühleisen J, Maurer HP, Stiewe G, Bury P, Rrif JC (2013) Hybrid breeding in barley. *Crop Science* 53: 819–824.
6. Qu Z, Li L, Luo J, Wang P, Yu S, Mou T (2012) QTL Mapping of combining ability and heterosis of agronomic traits in rice backcross recombinant inbred lines and hybrid crosses. *PLoS ONE* 7(1): e28463. doi: [10.1371/journal.pone.0028463](https://doi.org/10.1371/journal.pone.0028463) PMID: [22291881](https://pubmed.ncbi.nlm.nih.gov/22291881/)
7. Walejki RN, Russell WA (1977) Application of combining ability in plant breeding. *Crop Science* 17(4): 747–751.
8. Melchinger AE, Geiger HH, Seitz G, Schmidt GA (1987) Optimum prediction of three-way crosses from single crosses in forage maize (*Zea mays* L.). *Theor. Appl. Genet.* 74(3): 339–345. doi: [10.1007/BF00274716](https://doi.org/10.1007/BF00274716) PMID: [24241671](https://pubmed.ncbi.nlm.nih.gov/24241671/)
9. Gardner CO, Eberhart SA (1966) Analysis and interpretation of the variety cross diallel and related populations. *Biometrics* 22(3): 439–452. PMID: [5970549](https://pubmed.ncbi.nlm.nih.gov/5970549/)
10. Bagheri N, Jelodar NB (2010) Heterosis and combining ability analysis for yield and related—yield traits in hybrid rice. *International Journal of Biology* 2(2): 222–231.
11. Tiwari DK, Pandey P, Giri SP, Dwivedi JL (2011) Prediction of gene action, heterosis and combining ability to identify superior rice hybrids. *International Journal of Botany* 7(2): 126–144.
12. Abdel-Moneam MA, Attia AN, EL-Emery MI, Fayed EA (2009) Combining ability and heterosis for some agronomic traits in crosses of maize. *Pakistan Journal of Biological Sciences* 12(5): 433–438. PMID: [19579983](https://pubmed.ncbi.nlm.nih.gov/19579983/)
13. Gissa DW, Zelleke H, Labuschagne MT, Hussien T, Singh H (2007) Heterosis and combining ability for grain yield and its components in selected maize inbred lines. *South African Journal of Plant and Soil* 24(3): 133–137.
14. Gouda RK, Kage U, Lohithaswa HC, Shekara BG, Shobha D (2013) Combining ability studies in maize (*Zea Mays* L.). *Molecular Plant Breeding* 3(14): 116–127.
15. Li Y, Peng J, Liu Z (1997) Heterosis and combining ability for plant height and its components in hybrid wheat with triticum timopheevi cytoplasm. *Euphytica* 95(3): 337–345.
16. Krystkowiak K, Adamski T, Surma M, Kaczmarek Z (2009) Relationship between phenotypic and genetic diversity of parental genotypes and the specific combining ability and heterosis effects in wheat (*Triticum aestivum* L.). *Euphytica* 165(3): 419–434.
17. Madić MR, Djurović DS, Knezević DS, Paunović AS, Tanaskovic ST (2014) Combining abilities for spike traits in a diallel cross of barley. *Journal of central Europran Agriculture* 15(1): 108–116.
18. Zhou MX, Li HB, Chen ZH, Mendham NJ. Combining ability of barley flour pasting properties. *Journal of Cereal Science*, 2008, 48: 789–793.

19. Chen ZH, Sgabala S, Mendham N, Newman I, Zhang GP, Zhou MX. Combining ability of salinity tolerance on the basis of NaCl-induced K<sup>+</sup> flux from roots of barley. *Crop Science*, 2008, 48: 1382–1388.
20. Zhou MX, Li HB, Chen ZH, Mendham NJ. Combining ability of waterlogging tolerance in barley. *Crop Science*, 2007, 47: 278–284.
21. Frank H, Nadine H (2007) Towards the molecular basis of heterosis. *Trends in Plant Science* 12(9): 427–432. PMID: [17720610](#)
22. Xu RG, LV C, Zhu L, Zhou MX, Mo HD (2004) Studies on the heterosis of barley (*Hordeum vulgare* L.) I. Superiority of Hybrid F<sub>1</sub> from Mid-Parent or over Better-Parent. *Acta Agronomica Sinica* 30(7): 668–674.
23. Mo HD (1982) Combining ability analysis of p×q design. *Academic Journal of JiangSu Agriculture College* 3(3): 51–57.
24. Wricke G, Weber WE (1986) *Quantitative genetics and selection in plant breeding*. Berlin, New York: W. de Gruyter.